Wilson Bull., 102(4), 1990, pp. 672–683

BEHAVIOR, BODY CONDITION, AND FOODS OF BUFFLEHEADS AND LESSER SCAUPS DURING SPRING MIGRATION THROUGH THE KLAMATH BASIN, CALIFORNIA

JAMES H. GAMMONLEY AND MICKEY E. HEITMEYER[1]

ABSTRACT.—Behavior, body condition, and food habits of Buffleheads (*Bucephala albeola*) and Lesser Scaups (*Aythya affinis*) were studied in the Klamath Basin in northern California in spring 1986 and 1987. Peak Lesser Scaup and Bufflehead numbers were present in early February and mid-March, respectively. The first spring migrants of both species were mostly paired or courting adults. Buffleheads and Lesser Scaups spent 63–82% and 23–50% of their diurnal activities feeding, respectively. Both species consumed primarily (66–77% volume, 58–72% dry weight) invertebrates. Chironomidae larvae were the most important food consumed by both species. Body and carcass masses of both species were near mid-winter levels but below masses observed upon their arrival at northern breeding areas. Our data indicate that wetland habitats in the Klamath Basin provide important food and resting resources for migrating Buffleheads and Lesser Scaups. *Received 11 Sept. 1989, accepted 20 Mar. 1990.*

The biology of diving ducks (tribes Aythyini and Mergini) during spring migration is poorly documented. For some waterfowl species, habitat conditions on wintering and spring migration areas influence their ability to obtain nutrients required to meet the nutritional costs of migration, courtship, pairing, and molt (e.g., Heitmeyer 1988). Additionally, lipid and protein reserves stored during late winter and spring may influence the reproductive potential of Lesser Snow Geese (*Chen caerulescens*) (Ankney and MacInnes 1978, Wypkema and Ankney 1979, Davies and Cooke 1983), Canada Geese (*Branta canadensis*) (Raveling 1979), and Mallards (*Anas platyrhynchos*) (Krapu 1981, Heitmeyer 1988, LaGrange and Dinsmore 1988). In contrast, nutrient storage patterns of diving ducks are less well-known (but see Hohman et al. 1988).

The Klamath Basin in southern Oregon and northern California is a primary migration area used by many waterfowl in the Pacific Flyway, including Buffleheads (*Bucephala albeola*) and Lesser Scaups (*Aythya affinis*) migrating along intermountain corridors to breeding areas in western North America (Erskine 1972, Bellrose 1980). We collected data on habitat use, behavior, body condition, and food habits for Buffleheads and Lesser Scaups during spring migration through the Klamath Basin. These

[1] Dept. of Wildlife and Fisheries Biology, Univ. of California–Davis, Davis, California 95616 (Present address JHG: Gaylord Memorial Laboratory, Univ. Missouri-Columbia, Puxico, Missouri 63960; MEH: California Waterfowl Association, 3840 Rosin Court, Suite 200, Sacramento, California 95834).

data help describe the behavioral and physiological ecology of these species, and the importance of resources provided at this important migration stopover area.

STUDY AREA AND METHODS

Data were collected at Lower Klamath National Wildlife Refuge (LKNWR) located along the California-Oregon border. LKNWR contains 20,944 ha of shallow palustrine wetlands, grasslands, and croplands. Wetlands are managed primarily as permanently (PF) and seasonally flooded (SF) marshes. PF marshes are mostly 1–2 m deep and dominated by cattail (*Typha* spp.); hardstem "tule" bulrush (*Scirpus acutus*); many "moist-soil" species including alkali bulrush (*Scirpus robustus*), smartweeds (*Polygonum* spp.), common barnyard grass (*Echinochloa* spp.), dock (*Rumex* spp.), and various sedges; and sago pondweed (*Potamogeton pectinatus*). SF marshes are typically flooded <1 m deep from early fall (August–September) through spring (April–May) and are dominated by smartweeds, common barnyard grass, dock, sedges, foxtail (*Hordeum fueginus*), and goosefoot (*Chenopodium* spp.). Wetlands at LKNWR are approximately 45% SF and 55% PF. Other habitats on LKNWR include barley fields, grazed and ungrazed uplands, and vernal pools dominated by flixweed (*Descurainia sophia*) and saltgrass (*Distichlis spicata*). Rainfall in the Klamath Basin averages 15 cm during September–March and was near long-term means in 1985–1986 and 1986–1987 (U.S. Department of Commerce 1985–1987). Temperatures in the Klamath average 5°C and 7°C during February and March, respectively, and were near long-term means during this study.

Bufflehead and Lesser Scaup numbers on LKNWR from September through April 1985—1986 and 1986–1987 were estimated during aerial surveys conducted by LKNWR personnel. We observed and collected birds on LKNWR during 8–18 March 1986 and 24 February–18 March 1987.

We observed flocks during all daylight hours and recorded their activity using scan-sampling techniques (Altmann 1974). Scans were made in both PF and SF habitats selected opportunistically; both species were present in all but three scans. We repeatedly scanned a selected flock for at least 20 min. A total of 22.8 h of time-activity data, consisting of 172 scans was collected. Numbers of Buffleheads and Lesser Scaups observed per scan averaged 61 and 71, respectively. We recorded bird activity as follows: (1) feeding (included picking at foods on the surface, diving, and dive pauses); (2) resting (sleeping and loafing); (3) preening (also includes drinking and bathing); (4) locomotor (swimming and flight); (5) courtship (courtship displays, courtship flights, and copulations); and (6) agonistic (alert posture, intra- and inter-specific aggression). Determination of courtship displays followed Myres (1959), Johnsgard (1965), and Erskine (1972). Scan-sampling underestimates time spent feeding by diving ducks since birds cannot be observed while under water (Hohman 1984, Baldassarre et al. 1988). Although we scanned flocks at a slow rate in an effort to reduce this bias, our behavior data undoubtedly underestimate time spent feeding.

We used plumage characteristics (Palmer 1976) to determine sex ratios. A higher percentage of Buffleheads than recorded may have been male because females and immature males have similar plumage. Most juvenile Buffleheads migrate several weeks later in spring than adults (Erskine 1972). Therefore, our observations in early spring migration were likely only slightly biased toward females. Prior to or following each set of scans, we determined the pairing status (paired or unpaired) of female Buffleheads and Lesser Scaups from displays and association of the female with a male (Johnsgard 1965).

Buffleheads and Lesser Scaups were shot in both SF and PF habitats. Immediately following collection, the esophagus and proventriculus of each bird was removed and stored

in 95% ethanol for subsequent analyses of food habits. We sorted and identified contents of the esophagus and proventriculus within six months of collection. Food consumption is reported as frequency of occurrence, aggregate percentage volume, and aggregate percentage dry weight. Dry weight (nearest 0.001 g) of foods was determined after drying at 60°C for 24 h.

After collection and removal of esophagus and proventriculus, birds were frozen for later analyses of body composition. Birds were thawed within six months of collection and weighed, measured, plucked, and dissected. We determined molt status of collected birds using methods similar to Heitmeyer (1987). Internal organs were weighed to the nearest 0.1 g on a top-loading digital scale. Contents of the gizzard, intestines, and ceca were removed and body and organ masses adjusted for these contents. The eviscerated carcass (lacking liver, heart, spleen, gizzard, kidneys, and intestines) was subsequently homogenized in a meat grinder (McLandress and Raveling 1981). A carcass sample of approximately 50 g was oven dried at 100°C for 48 h. Following drying, each sample was weighed to determine moisture content and then placed in a Soxhlet apparatus and lipids extracted for 48 h using petroleum ether as a solvent. The lipid-free sample was then weighed and ashed in a muffle furnace at 650°C for 24 h. Ash weight was subtracted from the lipid-free sample weight to obtain the ash-free lean dry mass (AFLDM), a measure of protein content (Raveling 1979).

Satterthwaite's approximation of the *t*-test (Snedecor and Cochran 1980:97) was used to compare sex ratio and pairing data between habitat types for each year. Time spent in each activity was compared without pooling data between years, sexes, and habitat types for each species using Mann-Whitney *U*-tests (Daniel 1978). Mann-Whitney *U*-tests were also used to examine differences between sexes for body and nutrient reserve masses.

RESULTS

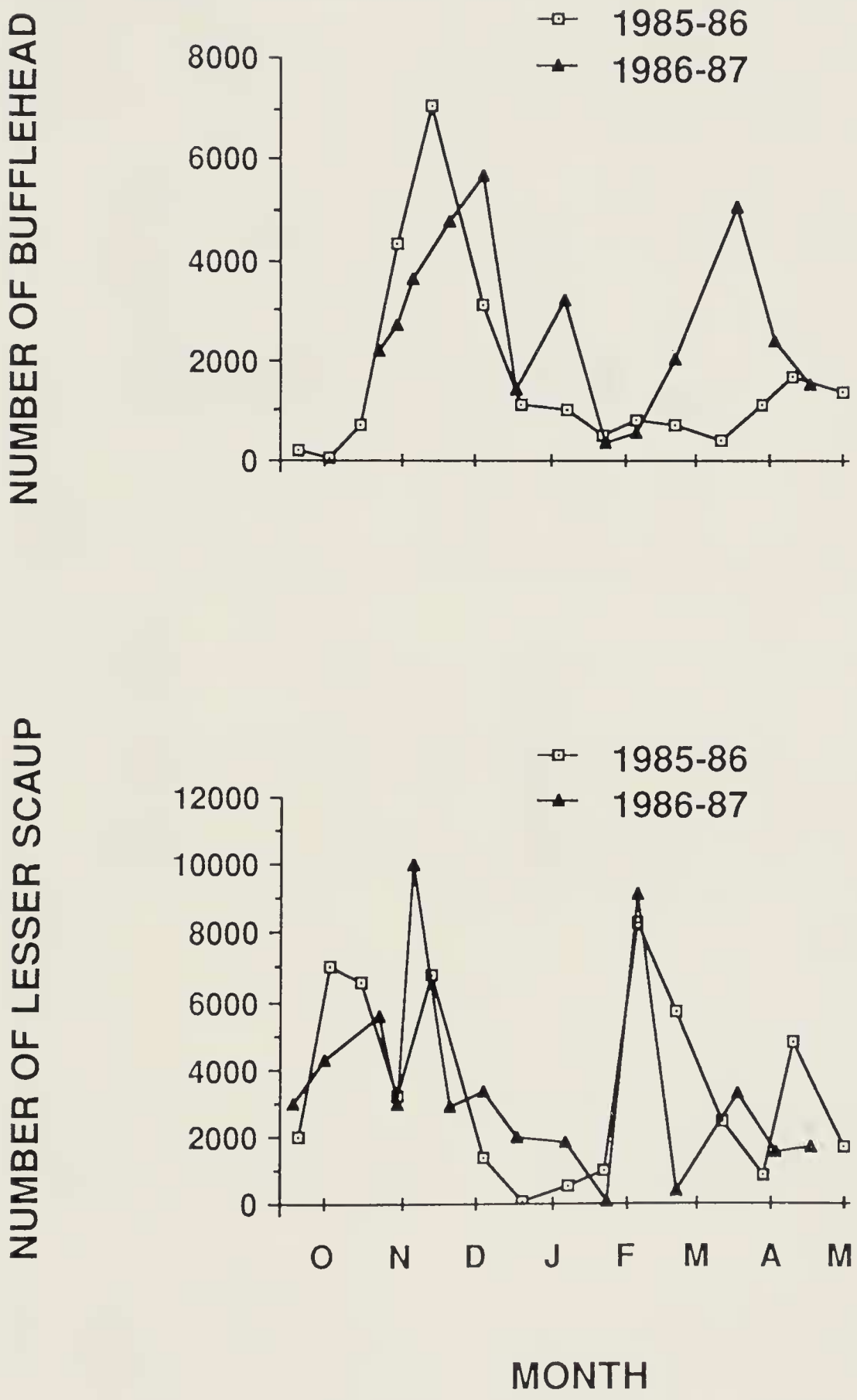
Migration chronology, sex and pairing status, and habitat use.—Lesser Scaups migrated through the Klamath Basin from September through mid-November in fall 1985 and 1986 and from late January through April in spring 1986 and 1987 (Fig. 1). Bufflehead migration into the Klamath Basin was later in both fall (peak numbers occurred during late November and early December) and spring (peak numbers from mid–March through mid-April) (Fig. 1).

Eighty percent of Buffleheads were found on SF wetlands, while 61% of Lesser Scaups were observed on PF wetlands. Typically, a higher proportion of males was present in flocks on PF than on SF habitats for both species ($P < 0.05$) except for Buffleheads in 1987 ($P > 0.05$) (Table 1). Approximately 50% of female Buffleheads and Lesser Scaups were paired from late February to mid-March (Table 1). The percentage of paired females was not different ($P > 0.05$) between PF and SF habitat types.

Time budgets.—Buffleheads spent >60% of the day feeding (Fig. 2). Time spent in various activities by Buffleheads was not different ($P >$

→

FIG. 1. Population estimates of Buffleheads and Lesser Scaups in the Klamath Basin, 1985–1986 and 1986–1987.


NUMBER OF BUFFLEHEAD
1985-86
1986-87
8000
6000
4000
2000
0
NUMBER OF LESSER SCAUP
1985-86
1986-87
12000
10000
8000
6000
4000
2000
0
O
N
D
J
F
M
A
M
MONTH

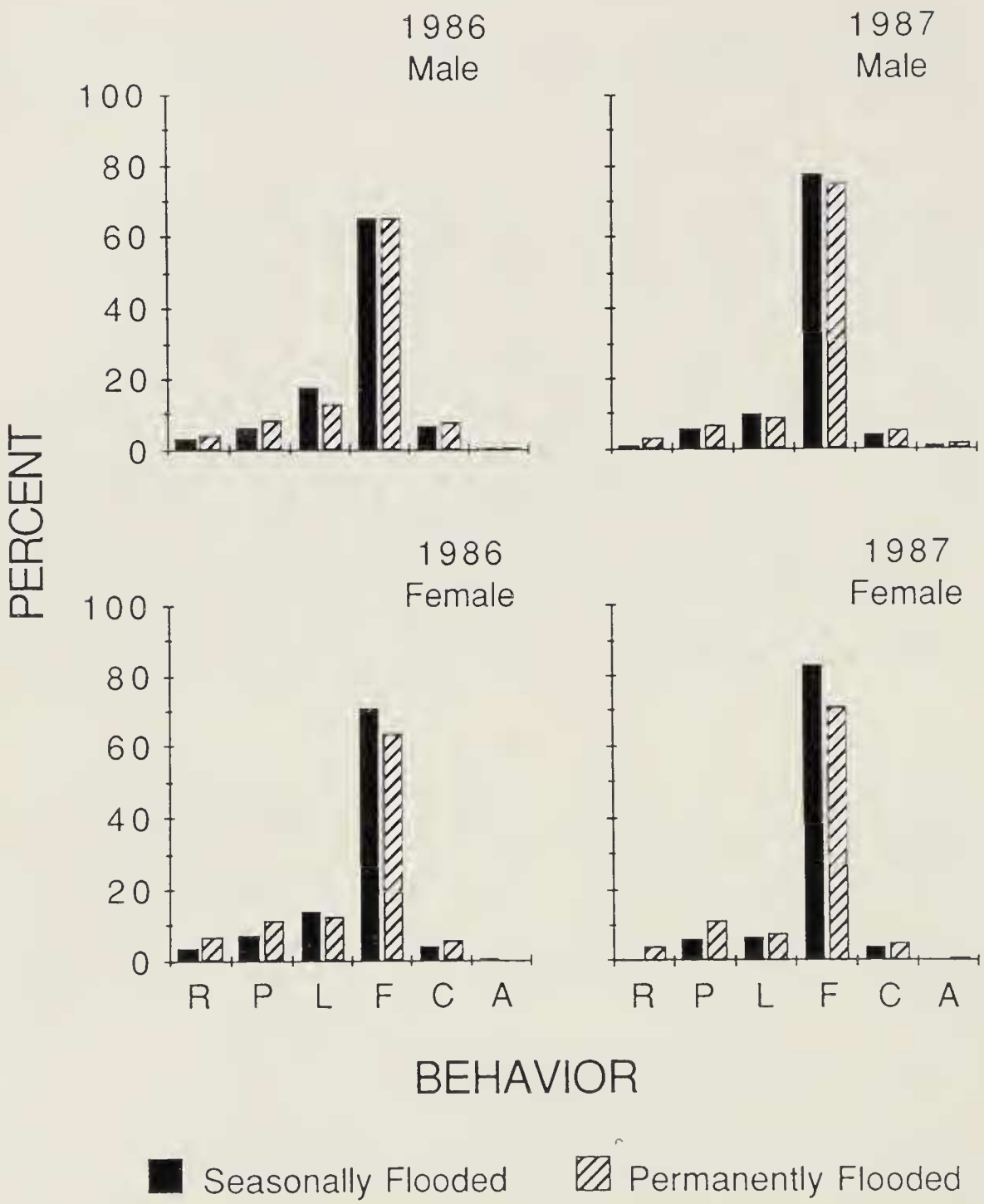


FIG. 2. Percentage of time spent by Buffleheads on seasonally and permanently flooded marshes at Lower Klamath National Wildlife Refuge in various activities during daylight hours. R = resting, P = preening, L = locomotor, F = feeding, C = courtship, and A = agonistic.

0.05) between years, sexes, or habitat types. Buffleheads were typically very active and spent little time (<10%) resting during daylight hours. Locomotor activity consisted mainly of birds swimming and flying to join feeding flocks or courtship parties. Three copulations were observed on

TABLE 1

PERCENTAGE OF MALES IN FLOCKS, AND PERCENTAGE OF FEMALES THAT WERE PAIRED, OF BUFFLEHEADS AND LESSER SCAUP OBSERVED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SEASONALLY FLOODED (SF) AND PERMANENTLY FLOODED (PF) HABITATS IN SPRING 1986 AND 1987

	Percentage male			Percentage female paired		
Species and year	SF	PF	Combined	SF	PF	Combined
Bufflehead						
1986	58.1	63.9	59.0	53.5	56.1	53.8
	(34)[a]	(29)	(63)	(38)	(30)	(68)
1987	62.1	62.0	62.1	51.9	54.0	52.1
	(54)	(49)	(103)	(52)	(49)	(101)
Lesser Scaup						
1986	70.1	78.5	74.2	48.6	50.7	49.4
	(34)	(31)	(65)	(35)	(29)	(64)
1987	68.2	72.4	71.4	52.7	55.0	54.4
	(51)	(50)	(101)	(51)	(49)	(100)

[a] Number of flocks sampled in parentheses.

TABLE 2

ESOPHAGEAL AND PROVENTRICULAR CONTENTS OF BUFFLEHEADS COLLECTED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SPRING 1986 AND 1987

	Males (N = 4)			Females (N = 7)			Combined (N = 11)		
Food item	O[a]	V	W	O	V	W	O	V	W
Animal	100	73	70	100	61	51	100	66	58
Chironomidae	100	13	12	86	28	18	91	22	16
Corixidae	25	40	29	43	21	14	36	29	20
Physidae	25	13	24	14	6	11	18	9	16
Planorbidae	25	2	2	14	1	4	18	2	3
Ostracoda	25	2	1	14	1	1	18	2	1
Gammaridae	25	2	1	14	1	tr	18	2	1
Dytiscidae				14	3	2	9	2	1
Plant (seeds)	75	27	30	86	39	49	82	34	42
Scirpus robustus	75	8	12	57	10	11	64	9	11
Polygonum lapathifolium	50	8	11	42	10	17	45	9	15
Scirpus acutus	50	4	4	14	3	2	27	3	3
Rumex spp.	75	4	1	14	1	tr	36	2	1
Potamogeton pectinatus	25	2	2	57	13	17	45	8	11
Chenopodium botrys	25	2	tr				9	1	tr
Carex spp.				14	1	tr	9	1	tr
Eleocharis spp.				14	1	tr	9	1	tr

[a] O = Percent occurrence, V = percent aggregate volume, W = percent aggregate dry weight, tr = trace.

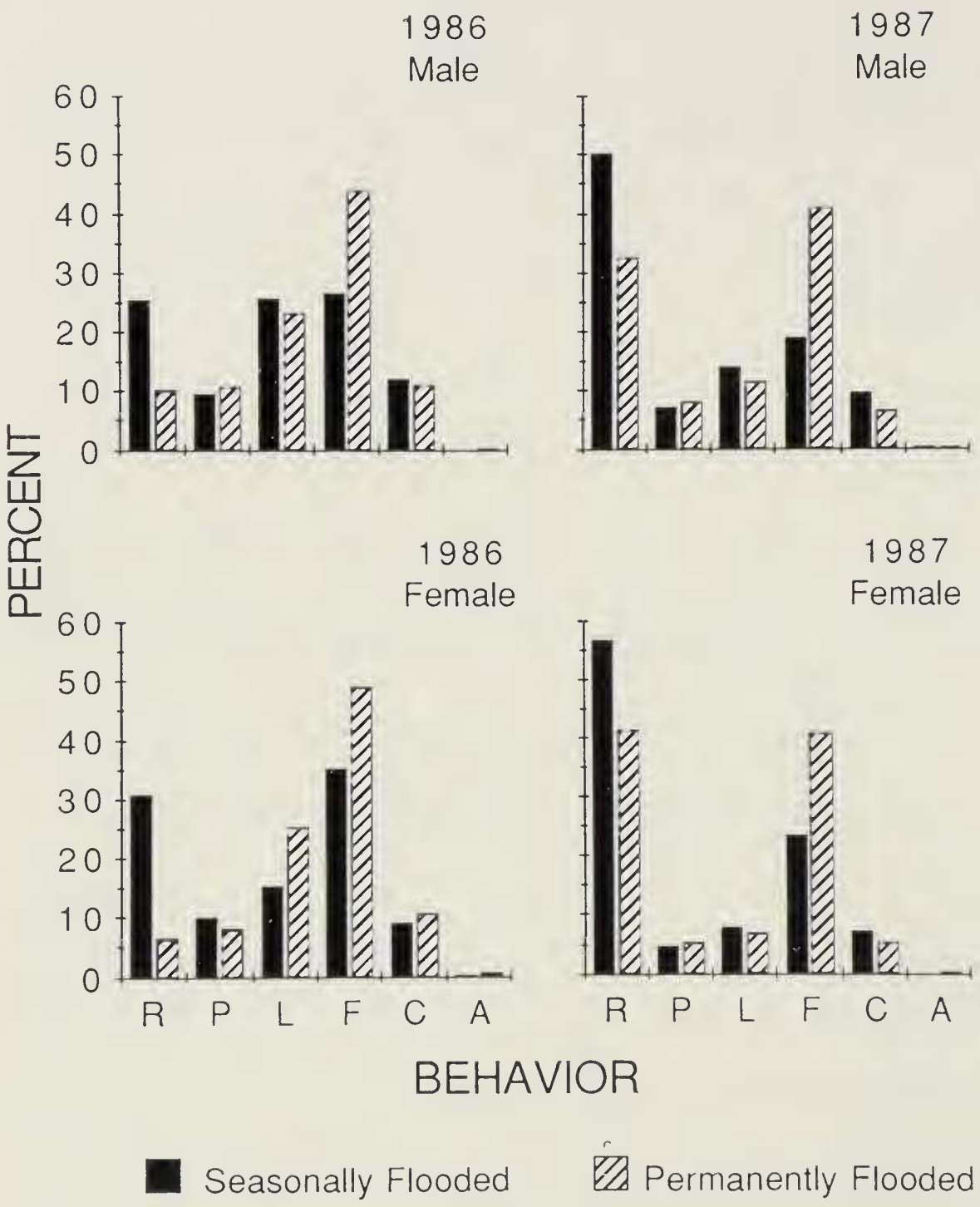


FIG. 3. Percentage of time spent by Lesser Scaups on seasonally and permanently flooded marshes at Lower Klamath National Wildlife Refuge in various activities during daylight hours. R = resting, P = preening, L = locomotor, F = feeding, C = courtship, and A = agonistic.

SF habitats. Common courtship activities included leading and following, head-bobbing, and pre- and post-copulatory displays. Aggressive interactions of males were mostly related to courtship.

Lesser Scaups spent more time resting and less time feeding during the

TABLE 3

ESOPHAGEAL AND PROVENTRICULAR CONTENTS OF LESSER SCAUPS COLLECTED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SPRING 1986 AND 1987

Food item	Males (N = 6)			Females (N = 5)			Combined (N = 11)		
	O[a]	V	W	O	V	W	O	V	W
Animal	100	82	85	100	70	61	100	77	72
Chironomidae	83	50	63	100	34	33	91	44	46
Ostracoda	17	28	20	20	2	1	18	18	9
Planorbidae	33	3	2	100	14	12	64	7	8
Copepoda				20	12	5	9	5	3
Dytiscidae	17	1	1	20	4	2	18	2	1
Physidae				20	2	7	9	1	4
Daphnidae				20	2	1	9	1	1
Gammaridae	17	tr	tr				9	tr	tr
Plant (seeds)	83	18	15	80	30	39	82	23	28
Potamogeton pectinatus	33	7	6	40	16	27	36	10	17
Polygonum lapathifolium	67	5	4	40	4	2	54	5	3
Scirpus robustus	17	3	3	40	6	8	27	4	5
Rumex spp.	17	1	1	20	2	1	18	2	1
Scirpus acutus				40	2	3	18	1	1
Chenopodium botrys	17	1	1				9	1	tr

[a] O = Percent occurrence, V = percent aggregate volume, W = percent aggregate dry weight.

day than Buffleheads (Fig. 3). Time spent in all activities was not different ($P > 0.05$) between male and female Lesser Scaups. Lesser Scaups spent more ($P < 0.05$) time (>40% of the day) feeding in PF habitats than on SF habitats (<30% of the day) (Fig. 3). In contrast, scaups spent more time ($P < 0.05$) resting in SF habitats than in PF habitats. Lesser Scaups rested more in 1987 than during 1986 in both habitats ($P < 0.05$). Courtship among scaups usually consisted of ≥5 males courting one female. Agonistic behaviors by scaups were rare.

Food habits.—Buffleheads and Lesser Scaups consumed primarily (77% and 66% dry weight, respectively) animal matter while in the Klamath Basin (Tables 2, 3). Midge larvae (Chironomidae) were the most frequently consumed invertebrates and were present in 91% of both Buffleheads and scaups. Other foods commonly consumed by Buffleheads were water boatmen (Corixidae), physid snails (Physidae), and seeds of smartweed, alkali bulrush, and sago pondweed (Table 2). Lesser Scaups consumed many ostracods (Ostracoda), planorbid snails (Planorbidae), and sago pondweed seeds in addition to chironomids (Table 3).

Body condition.—All male Buffleheads and Lesser Scaups collected were paired, non-molting, and in Alternate plumage. All female Lesser Scaups

TABLE 4

CARCASS AND SELECTED ORGAN MASSES (MEANS ± SE IN G) OF BUFFLEHEADS AND LESSER SCAUPS COLLECTED ON LOWER KLAMATH NATIONAL WILDLIFE REFUGE IN SPRING 1986 AND 1987

	Bufflehead		Lesser Scaup	
	(N = 6) Male	(N = 7) Female	(N = 6) Male	(N = 5) Female
Fresh body	442 ± 37	333 ± 21*[a]	734 ± 24	663 ± 52*
Eviscerated carcass	311 ± 15	215 ± 21*	499 ± 34	438 ± 22*
Moisture	192 ± 19	136 ± 5*	298 ± 20	279 ± 17
Lipid	40 ± 15	26 ± 15*	78 ± 9	53 ± 27
Ash	10 ± 3	6 ± 2	17 ± 3	14 ± 1
AFLDM	70 ± 7	48 ± 5*	108 ± 5	92 ± 5
Right breast	37 ± 2	27 ± 2*	63 ± 3	58 ± 4
Right leg	16 ± 1	12 ± 1*	27 ± 5	24 ± 2
Liver	15 ± 3	12 ± 2	19 ± 1	19 ± 2
Gizzard	10 ± 3	8 ± 2	29 ± 1	26 ± 7
Intestine	12 ± 3	10 ± 1	31 ± 4	31 ± 4
Testes or ovary	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	0.2 ± 0.1
Oviduct		0.3 ± 0.1		0.2 ± 0.2

[a] Mann-Whitney *U*-tests (Daniel 1978) between sexes, * = $P < 0.05$.

were paired and in early stages of the prebasic molt. Five of the six female Buffleheads collected were paired and in early stages of the prebasic molt; the other female Bufflehead was paired, non-molting,and in Alternate plumage.

Absolute measures of body, eviscerated carcass, and moisture masses were larger for male than for female Buffleheads and Lesser Scaups; other organ and carcass composition masses were similar between sexes in both species except for lipid, AFLDM, right breast, and right leg masses in Buffleheads (Table 4). Buffleheads averaged 26–40 g lipid, while Lesser Scaups averaged 53–78 g lipid. Gonad and oviduct masses were small for both species.

DISCUSSION

Migration chronology of Buffleheads and Lesser Scaups through the Klamath Basin during our study was similar to that reported by Erskine (1972) and Bellrose (1980). Sex ratios observed in this study were also similar to those reported in other studies (Bellrose et al. 1961, Erskine 1972, Bellrose 1980). The percentage of paired females was generally higher, however, than reported for early spring in other studies and locations (Weller 1965, Erskine 1972). Our study occurred relatively early in spring migration for both species (Erskine 1972, Bellrose 1980) and all

but one of the birds we collected were adults; therefore, it appears that a large proportion of the first Buffleheads and Lesser Scaups migrating northward into the Klamath Basin in spring were paired adults. Earlier northward migration in spring by paired adults has been documented for some other waterfowl species, and may confer survival and reproductive potential advantages (McLandress and Raveling 1981, Heitmeyer 1988).

Wetland habitats in the Klamath Basin provide important food resources and resting areas for Buffleheads and Lesser Scaups. Spring migrant female Buffleheads and scaups incur overlapping nutritional costs of migration, courtship, and prebasic molt, and both species spent considerable portions of the day feeding. High consumption of invertebrates by Buffleheads and scaups in this study is consistent with other winter and spring food habits data for both species (Yocum and Keller 1961, Rogers and Korschgen 1966, Bartonek and Hickey 1969, Erskine 1972, Hoppe et al. 1986). Invertebrates, and chironomid larvae in particular, are heavily exploited by several waterfowl species (Gray 1980, Pederson and Pederson 1983, Woodin and Swanson 1989).

Relatively little is known about body and organ masses and nutrient storage patterns of diving ducks. Although sample sizes are small, data for this study suggest that Bufflehead and Lesser Scaup body masses in the Klamath Basin during spring are near winter levels (Ryan 1972, Joanen 1964, Erskine 1972) but below body masses upon arrival at northern breeding areas (Erskine 1972; Afton and Ankney unpubl.). However, comparative data for wintering or breeding scaup populations in the Pacific Flyway are needed for accurate interpretations of spring body mass data.

The above considerations emphasize the importance of spring migration sites, such as the Klamath Basin, to Buffleheads and Lesser Scaups. The continued loss of wetland habitats throughout North America (Tiner 1984) amplifies the need for enhanced management of high quality habitats on remaining areas. Further studies of diving ducks on spring migration areas are needed to elucidate evolutionary factors influencing chronology of annual events, patterns of nutrient storage, habitat use, and behavior.

ACKNOWLEDGMENTS

Funding for this study was provided by the California Waterfowl Association, Delta Waterfowl and Wetlands Research Station, and the University of California–Davis. We kindly thank the staff of the Klamath Basin National Wildlife Refuge complex, especially J. Hainline and H. McCollum, for providing access and assistance throughout the study. B. Dugger and K. Lumas-Dugger assisted with laboratory analyses. A. Afton and D. Ankney kindly allowed us to cite their unpublished ms. on body composition of breeding Lesser Scaup. A. Afton, J. Austin, L. Fredrickson, J. Hainline, J. Kelley, R. McLandress, D.

Raveling, F. Reid, and M. Tome provided many valuable suggestions for improving an earlier draft of the manuscript.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227–267.

ANKNEY, C. D. AND C. D. MACINNES. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459–471.

BALDASSARRE, G. A., S. L. PAULUS, A. TAMISIER, AND R. D. TITMAN. 1988. Workshop summary: techniques for timing activity of wintering waterfowl. Pp. 181–188 *in* Waterfowl in winter (M. W. Weller, ed.). Univ. Minnesota Press, Minneapolis, Minnesota.

BARTONEK, J. C. AND J. J. HICKEY. 1969. Selective feeding by juvenile diving ducks in summer. Auk 86:443–457.

BELLROSE, F. C. 1980. Ducks, geese, and swans of North America. 3rd ed. Stackpole Books, Harrisburg, Pennsylvania.

———, T. G. SCOTT, A. S. HAWKINS, AND J. B. LOW. 1961. Sex ratios and age ratios of North American ducks. Ill. Nat. Hist. Sur. Bull. 27:391–474.

DANIEL, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Company, Boston, Massachusetts.

DAVIES, J. C. AND F. COOKE. 1983. Annual nesting productivity in Snow Geese: prairie droughts and arctic springs. J. Wildl. Manage. 47:291–296.

ERSKINE, A. J. 1972. Buffleheads. Can. Wildl. Serv. Monogr. Ser. 4. Ottawa, Ontario.

GRAY, B. J. 1980. Reproduction, energetics, and social structure of the Ruddy Duck. Ph.D. diss., Univ. Calif., Davis, California.

HEITMEYER, M. E. 1987. The prebasic moult and basic plumage of female mallards (*Anas platyrhynchos*). Can. J. Zool. 65:2248–2261.

———. 1988. Body composition of female Mallards in relation to annual cycle events. Condor 90:669–680.

HOHMAN, W. L. 1984. Diurnal time-activity budgets for Ring-necked Ducks wintering in central Florida. Proc. Annu. Conf. Southeast. Assoc. Fish and Game Comm. 38:158–164.

———, T. S. TAYLOR, AND M. W. WELLER. 1988. Annual body weight change in Ring-necked ducks. Pp. 257–269 *in* Waterfowl in winter (M. W. Weller, ed.). Univ. Minnesota Press, Minneapolis, Minnesota.

HOPPE, R. T., L. M. SMITH, AND D. B. WEBSTER. 1986. Foods of wintering diving ducks in South Carolina. J. Field Ornithol. 57:126–134.

JOANEN, T. 1964. Methods and trap design for Lesser Scaup trapping in Louisiana. Proc. Southeast. Assoc. Game and Fish Comm. 18:106–109.

JOHNSGARD, P. A. 1965. Handbook of waterfowl behavior. Cornell Univ. Press, Ithaca, New York.

KRAPU, G. L. 1981. The role of nutrient reserves in Mallard reproduction. Auk 98:29–38.

LAGRANGE, T. G. AND J. J. DINSMORE. 1988. Nutrient reserve dynamics of female Mallards during spring migration through central Iowa. Pp. 287–297 *in* Waterfowl in winter (M. W. Weller, ed.). Univ. Minnesota Press, Minneapolis, Minnesota.

MCLANDRESS, M. R. AND D. G. RAVELING. 1981. Changes in diet and body composition of Canada Geese before spring migration. Auk 98:65–79.

MYRES, M. T. 1959. Display behavior of Buffleheads, scoters and goldeneyes at copulation. Wilson Bull. 71:159–168.

PALMER, R. S. 1976. Handbook of North American birds. Vol. 3. Yale Univ. Press, New Haven, Connecticut.

PEDERSON, G. B. AND R. L. PEDERSON. 1983. Feeding ecology of Pintails and Mallards on Lower Klamath marshes. Final Report to U.S. Fish and Wildl. Serv., Humboldt State Univ., Arcata, California.

RAVELING, D. G. 1979. The annual cycle of body composition of Canada Geese with special reference to control of reproduction. Auk 96:234–252.

ROGERS, J. P. AND L. J. KORSCHGEN. 1966. Foods of Lesser Scaups on breeding, migration, and wintering areas. J. Wildl. Manage. 30:258–264.

RYAN, R. A. 1972. Body weight and weight changes of wintering diving ducks. J. Wildl. Manage. 36:759–765.

SNEDECOR, G. W. AND W. G. COCHRAN. 1980. Statistical methods. 7th ed. Iowa State Univ. Press, Ames, Iowa.

TINER, R. W. 1984. Wetlands of the United States: current status and recent trends. U.S. Fish Wildl. Serv., Natl. Wetlands Inventory, Washington, D.C.

U.S. DEPARTMENT OF COMMERCE. 1985–1987. Climatological data, California. Vols. 89–91. Nat. Oceanic and Atmos. Admin., Nat. Climatic Center, Asheville, North Carolina.

WELLER, M. W. 1965. Chronology of pair formation in some Nearctic *Aythya* (Anatidae). Auk 82:227–235.

WOODIN, M. C. AND G. A. SWANSON. 1989. Foods and dietary strategies of prairie-nesting Ruddy Ducks and Redheads. Condor 91:280–287.

WYPKEMA, R. C. AND C. D. ANKNEY. 1979. Nutrient reserve dynamics of Lesser Snow Geese staging at James Bay, Ontario. Can. J. Zool. 57:213–219.

YOCUM, C. F. AND M. KELLER. 1961. Correlation of food habits and abundance of waterfowl, Humboldt Bay, California. Calif. Fish and Game 47:41–53.